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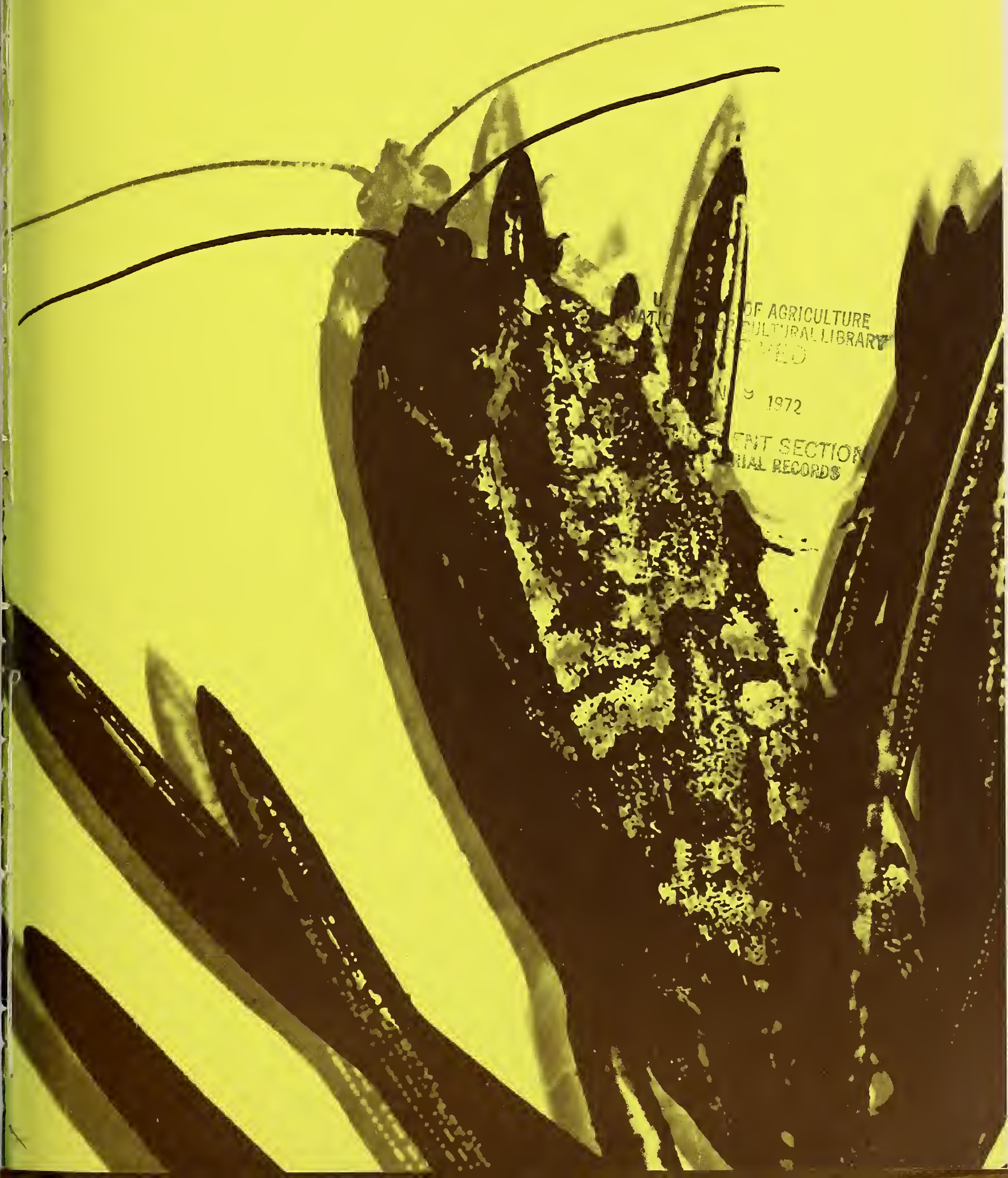
NATURAL MORTALITY OF THE WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS*, IN COLORADO

by M. E. McKnight



ABSTRACT

Most outbreaks of the western spruce budworm (Choristoneura occidentalis Freeman) in the central and southern Rocky Mountains are eventually terminated by natural causes. This study was initiated to identify and determine the relative importance of natural mortality factors. Life tables were prepared for two generations of budworms at three locations on two host species. Relationships between survival rates, fecundities, and sex ratios as dependent variables and budworm densities, survival from parasitism and predation, measures of food supply, and survivals in age-intervals as independent variables were analyzed by multiple regression. Considerable mortality was credited to unknown factors, possibly including infestation-induced changes in food quantity and quality, and weather. Mortality due to these factors was much higher in decreasing populations than in increasing.

Key words: Choristoneura occidentalis, western spruce budworm.

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by

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FOREWORD

To plan the protection of forest resources, the land manager should be able to predict the trends of pest populations accurately. He cannot afford costly control programs against outbreaks which would have collapsed of natural causes, nor can he delay the protection of valuable stands on the chance that the outbreak will terminate before the damage becomes intolerable. A fuller knowledge of the regulators of pest populations is needed to provide the essential evaluation procedures.

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INTRODUCTION

Outbreaks of the western spruce budworm, Choristoneura occidentalis Freeman (Lepidoptera: Tortricidae), are common in the mixed conifer stands of the central and southern Rocky Mountains. Most are of short duration and remain localized; others may persist for 10 years or longer and spread over thousands of acres.

Most outbreaks, small and large, are terminated by identifiable natural factors. Sometimes a late spring freeze kills the new buds or expanded shoots, and the budworm larvae starve without their preferred food. This probably halted a 14-year outbreak in Cody Canyon on the Shoshone National Forest in Wyoming in 1936. A similar freeze helped end an infestation which spread over the Front Range forest of Colorado from 1935 to 1945.

However, some outbreaks disappear even though great numbers of larvae are present in apparently good health. In 1946, larvae were abundant in June in an infestation near LaVeta Pass on the San Isabel National Forest. A month later no larvae and very few pupae could be found; in August the needles on more than 600 linear feet of Douglas-fir branches were examined without finding a budworm egg mass.

Similarly, larvae and pupae were very abundant in June and July 1962 in research plots on the Pike and Roosevelt National Forests. These areas were part of an outbreak which encompassed about 640,000 acres in Colorado that year. No new egg masses were found in those areas in August, and, in most other infestations in Colorado, densities of new egg masses were at their lowest levels since the outbreak began its general spread in 1958 and 1959. In 1963, a braconid, Bracon politiventris (Cush.) (Hymenoptera: Braconidae), normally rare, was abundant in some areas. It was perhaps the final factor to eliminate populations from specific locations. The collapse of the outbreak seemed to be initiated by the greatly reduced egg deposition in 1962.

This study was undertaken to achieve a better understanding of regulators of budworm populations.

METHODS

The Study Areas

Three principal study areas were established on the San Isabel National Forest. The Ophir Creek I area in the Wet Mountain Range, and the Balman Reservoir area about 50 miles away on the eastern slope of the Sangre de Cristo Range, represented mature and overmature stands (about 90 and 120 years old, respectively) consisting mainly of Douglas-fir (Pseudotsuga menziesii var. glauca), and white fir (Abies concolor). The Ophir Creek II area, about 1 mile from the Ophir Creek I area, represented young stands (about 40 years old) of white fir and Engelmann spruce (Picea engelmanni) under an aspen (Populus tremuloides) overstory.

At the beginning of each budworm generation, 10 trees of each of two host species were selected in each study area. Each such group of 10 trees constituted a "plot," and data were obtained from each plot in each study area for the 1964-65 and the 1965-66 generations of budworms.

At each sampling time, two branches about 24 inches long were taken from the middle one-third of the crown of each sample tree (fig. 1). The measured length and width of the foliated area of each branch were used to calculate foliage area, which was regarded as a factor to equate branches of different sizes. The density of the budworm population was calculated by dividing the total count of insects by the total foliage area (in 100 square inches) examined.

Hygrothermographs were installed about 25 feet aboveground in Douglas-fir trees. Four moth traps baited with virgin female moths were installed at the same places each year to record the activity of male moths.

Figure 1.--Samples of foliage were gathered in a basket on the pole pruner. The foliage was examined for larvae and pupae in the field, but egg masses were counted in the laboratory.

Preparation of Life Tables

Changes in budworm density were recorded in life tables prepared according to the techniques described by Morris and Miller (1954) with some modification as suggested by V. M. Carolin.[2] Table 1 is a mean life table based on the 12 life tables prepared, one for each of two generations on two host tree species at the three study areas (McKnight 1967).

[2] *Principal Entomologist, Pacific Northwest Forest and Range Exp. Sta., Portland, Oregon.*

Table 1.--Mean life table for two generations of the western-spruce budworm on six plots on the San Isabel National Forest

Age-interval, X	Number alive per 100 square inches, N_X, at beginning of X	Factor responsible for mortality, M_X	M_X as percentage of N_X	Survival rate, S_X, within X	Real mortality, M_X/N_E
Egg through instar III	30.97	Parasitoids	1.0		
		Other	34.1		
		All	35.1	0.649	0.351
Instar IV through V	20.10	Parasitoids	20.0		
		Other	31.8		
		All	51.8	.482	.336
Instar VI through early pupa	9.69	Parasitoids	20.8		
		Predators	1.1		
		Other	37.1		
		All	59.0	.410	.185
Pupa	3.97	Parasitoids	8.4		
		Predators	5.0		
		Other	6.1		
		All	19.5	.805	.025
Moth	3.20	Sex ratio P♀ = 0.45	10.0	.900	.010
Females × 2	2.88	Reduced fecundity	39.8	.602	.037
"Normal" females × 2	1.73	Adult mortality ± dispersal	66.9	.331	.037
Actual females × 2	.57				
Generation			98.2	.018	.982

Expected eggs: 222.34 = 154.4 eggs × 1.44 females
Actual eggs: 44.00 Maximum fecundity recorded: 256.5 eggs

Index of population trend: Expected 718 percent; Actual 142 percent

Notation

The symbols used in the life tables and the analyses are defined as follows:

N_X Population density of the western spruce budworm, expressed as the number of insects per 100 square inches of foliage, at the beginning of any age-interval X. N_E, N_{IV}, N_{VI}, N_P, N_M represent the number of eggs, instar IV larvae, instar VI larvae, "late" pupae, and moths, respectively.

M_X The number of budworms dying in any age-interval X.

S_X The percentage of budworms surviving in any age-interval X.

n A generation of the western spruce budworm.

n+1 The generation following n.

D_n The percent loss of needles from new-growth shoots in the year in which larvae of generation n mature.

M_i M_{par} and M_{pred} represent mortality caused by parasites or predators, respectively.

S_i S_{par} and S_{pred} represent survival from parasitism or predation, respectively.

Age-intervals

The decrease in population density from one sampling time to the next was termed "mortality." The samplings were timed to delimit appropriate age-intervals which encompassed significant instars, life stages, or biological events.

The "egg through instar III" age-interval.— Counts of egg masses were converted to counts of eggs, N_E, from estimates of the average number of eggs per mass or by the use of egg mass regressions (McKnight 1969). The difference between N_E and N_{IV} was M_E. $S_E = N_{IV}/N_E = 0.649$.[3]

The "instar IV through V" age-interval.— The sampling was made when the larvae had established their feeding sites in opening buds, usually when instar IV predominated. About half the sample of larvae was reared (fig. 2) to determine the percentage of parasitism by Apanteles sp. and Glypta fumiferanae (Vier.). The difference between N_{IV} and N_{VI} was the total mortality for this age-interval. Mortality

[3] *See corresponding* S_X *survival percentages in table 1.*

Figure 2.--Larvae of the western spruce budworm were reared on foliage in trays (A). Cocoons of parasitoids and budworm pupae were held in vials on wall racks (B) until adults emerged.

due to parasitoids was determined from the rearings and the remainder was due to "other" causes. $S_{IV} = N_{VI}/N_{IV} = 0.482$.

The "instar VI through early pupa" age-interval.—The sampling was made when about 40 percent of the budworm population had pupated, and the dipteran parasitoids had completed their attack against the larvae but no mortality had occurred. Larvae and pupae from the sample were held for emergence of parasitoids or moths, which were used in fecundity trials (fig. 3). The N_{VI} was the number of larvae and pupae in the sample. Total mortality during the age-interval was the difference between N_P and N_{VI} reduced by the percent mortality in the reared sample due to Apanteles sp. and Glypta fumiferanae, $S_{VI} = N_P/N_{VI} = 0.410$.

The "pupa" age-interval.—The sampling was made when 60 to 80 percent of the moths had emerged, and attack of the pupae by parasitoids was considered complete. Living pupae were held for emergence of parasitoids or moths. The moths were used in fecundity trials. Mortality due to Hymenoptera was tallied in this age-interval. The number of pupae killed by Diptera and the number of empty pupal cases showing holes left by escaping dipterans were ignored because this mortality was tallied in the previous age-interval. Pupal cases damaged by predators such as birds or budworm larvae were tallied. N_P was the sum of the N_M plus the density of parasitized pupae from the rearing (ignoring Diptera) plus the density of pupae damaged by predators. $S_P = N_M/N_P = 0.805$.

The "moth" age-interval.—The density of moths, N_M, was the sum of the number of pupal cases showing normal emergence of moths at the time of sampling in the pupa age-interval plus the number of moths emerging in the collection.

Females × 2.—The N_X was two times the product of the percentage females and N_M. The effect of an unequal sex ratio, $P_♀$ (0.900), was tallied in the "moth" age-interval.

"Normal" females × 2.—The N_X was computed from the N_X for the females × 2 age-interval times the ratio between the mean fecundity and maximum fecundity recorded in the fecundity trial. (This maximum fecundity differs from the theoretical F that Morris (1963) used as the maximum fecundity per female of a budworm population.) The effect of reduced fecundity, P_F (0.602), was tallied in the females × 2 age-interval.

Actual females × 2.—The N_X was computed from the number of eggs (counted in August) divided by the mean fecundity (from fecundity trials) times 2. This computation allows for adult mortality and dispersal into and out of the area. Morris (1963) used the theoretical F instead of mean fecundity. S_M = actual females × 2/"normal" females × 2 = 0.331.

Expected eggs and actual eggs.—The expected density of eggs was calculated from the mean fecundity times the number of females (N_M times $P_♀$). The actual density of eggs was measured in August.

Index of population trend.—These indices are comparisons of expected and actual numbers of eggs to the density of eggs at the beginning of the generation, expressed as percentages.

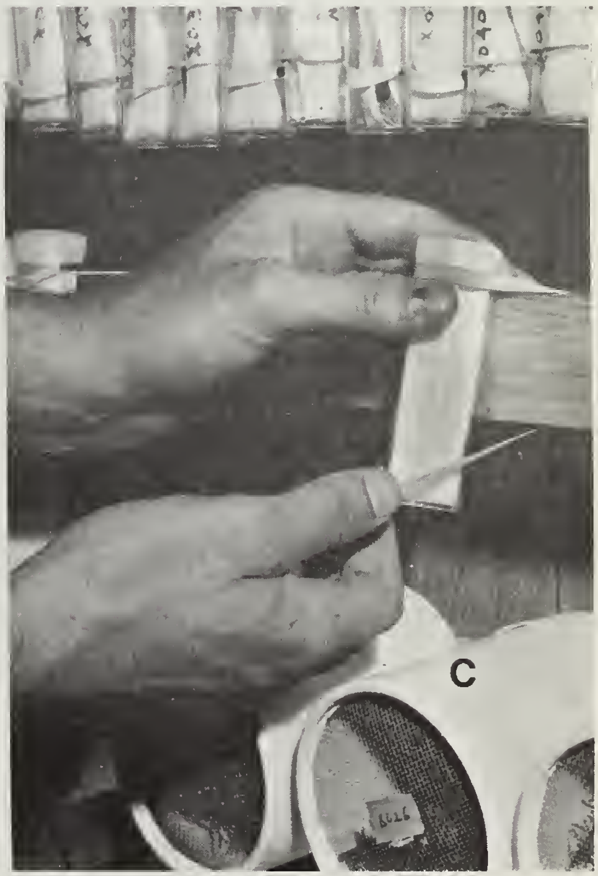
Estimation of Absolute Densities

To estimate the survival of moths, it was necessary to express budworm numbers as absolute densities, or numbers per unit of land area. Morris (1955) described computations to estimate absolute densities using cone volume, estimated from d.b.h., and branch surface regressions. Similar regressions were computed from data from the Ophir Creek I study area. Crown lengths and widths were obtained from Douglas-fir, white fir, and Engelmann spruce trees. The crowns were regarded as cones and their volumes were computed. Measurements of branch surface were obtained from felled Douglas-fir trees. The density of each tree species and the mean diameters were available from the stand description.

Techniques of Analysis

Data in the life tables were analyzed by methods similar to those of Morris (1963) and coworkers. Survival rates, sex ratios, and fecundities (transformed to log 10,000 S_X, log 10,000 $P_♀$, log 10,000 P_F, respectively) were treated as dependent variables in stepwise multiple regression analyses. Budworm densities, survivals from parasitism and predation (transformed to log 10,000 S_i), measures of food supply, and survivals in age-intervals (transformed) were treated as independent variables.

Figure 3.--Fecundity trials were conducted by confining paired moths with foliage in cages (A) affixed to racks in the rearing room of the laboratory trailer. Needles bearing egg masses were collected (B), the eggs were counted, and the egg masses were held in sleeves of gauze in plastic vials (C).



RESULTS

Survival in the "Egg Through Instar III" Age-interval (S_E)

D_{n-1}, the defoliation caused by larvae of the preceding generation, was evaluated as a variable affecting S_E because instar II larvae seldom mine needles more than 1 year old. N_E was used as another independent variable. Few observations of parasitism of eggs were available; therefore, N_E was corrected for parasitism by dividing S_E by $(N_E - M_{par})/N_E$ on those plots where parasitism of eggs was observed.

The multiple regression analysis indicated that S_E was significantly correlated with log N_E but not with D_{n-1}, and that the two independent variables were not significantly related. The model $S_E = 9.21 - 1.01 \log N_E$ accounted for about 84 percent of the variation in S_E.

The population density increased and S_E declined from the 1964-65 generation to the 1965-66 generation on five of the six plots. N_E averaged 18 eggs in 1964 and 48 in 1965; S_E dropped from 0.906 to 0.301. On the Douglas-fir plot at Balman Reservoir, N_E dropped from 28 in 1964 to 11 in 1965; S_E increased from 0.816 to 0.932.

The model for S_E suggests that survival of this age-interval is density-dependent—the more eggs, the lower the survival. The degree to which the instar I and II larvae are dispersed may be a function of the number of larvae moving about on the foliage and stimulating each other to drop by their threads. The occurrence of wind in this period must be an important factor.

Survival in the "Instar IV Through V" Age-interval (S_{IV})

Instar IV and V larvae should be most affected by factors related to food, parasitism, and rate of development. No data were available concerning the number of new shoots available to instar IV larvae. However, an index of food quantity (N_N) was computed as the product of the average millimeters of shoot growth (G) times the average number of needles per millimeter (N). These data were taken at the end of the growing season as part of the defoliation analysis for each plot.

Parasitism, largely by *Apanteles fumiferanae* Vier. and *Glypta fumiferanae*, was carefully evaluated throughout the study, and good data were available for most plots. $S_{par} = 1 - M_{par}$ was computed for each plot.

Multiple regression analyses failed to show significant relationships between density of larvae, food supply, or parasitism and S_{IV}, or between the independent variables themselves.

The data and the analyses suggest that S_{par} which ranged from about 69 percent to about 87 percent, was not a significant mortality factor in this age-interval. S_{IV} decreased on four of the six plots from the 1964-65 generation to the 1965-66 generation. On those four plots, mortality due to unidentified factors was high, from 42 percent to 71 percent in the 1965-66 generation; this mortality was low, from 17 percent to 21 percent, on the two plots on which S_{IV} increased.

The availability of food must certainly be one of the most important factors influencing survival during this age-interval. The analysis indicated that lengths of individual shoots and the numbers of needles on each were not related to S_{IV}, but there were no data to evaluate the numbers of shoots available. Future study of this age-interval should include counts of shoots at the time of sampling for N_{IV}.

Survival in the "Instar VI Through Early Pupa" Age-interval (S_{VI})

Population density, parasitism, and food availability were evaluated as independent variables. Because few assessments of predation were available, S_{VI} was corrected for predation by dividing S_{VI} by $(N_{VI} - M_{pred})/N_{VI}$.

Multiple regression analyses indicated that the model $S_{VI} = 2.29\ {}_{VI}S_{par} - 0.48\ N_{VI}^{-1}$ explained about 76 percent of the variation in S_{VI}. Only N_{VI}^{-1} was significantly correlated with S_{VI}; none of the independent variables were correlated with each other.

S_{VI} decreased on all six plots from the 1964-65 generation to the 1965-66 generation. Mortality due to parasitoids decreased on three plots. Mortality due to unidentified factors increased on five plots.

Parasitism was low, about 7 percent, for both generations on Engelmann spruce in the Ophir Creek II area. Mortality due to parasitoids varied from 10 percent to 35 percent on the other plots.

Several species of Diptera attack larvae during instar VI and kill their hosts shortly before or after pupation (McKnight 1968). Both *Madremyia saundersii* (Will.) and *Omotoma*

fumiferanae (Tot.) deposit macro-type eggs on the integument of instar VI larvae. Eggs of Ceromasia auricaudata Tns. are deposited on the foliage and eaten by instar VI larvae. The hosts do not die until pupation. C. auricaudata was the most important parasitoid at the Balman Reservoir area and on Douglas-fir at Ophir Creek I, but M. saundersii caused more mortality on white fir. O. fumiferanae was the most abundant parasitoid on both species of host trees at Ophir Creek II.

Immobile prepupae and pupae are subject to predation by larvae of the spruce coneworm, Dioryctria reniculella (Grote) (Lepidoptera: Phycitidae) (Warren 1954) and instar VI budworm larvae. This predation can be expected to increase when defoliation is severe and new foliage is scarce.

Survival in the "Pupa" Age-interval (S_P)

Parasitism and predation, expressed as $pS_{par} = 1\text{-}M_{par}$ and $pS_{pred} = 1\text{-}M_{pred}$, were tested as independent variables against S_P, the dependent variable. Multiple regression analysis indicated that pS_{par} and pS_{pred} were correlated with S_P, and with each other. The model

$S_P = 1.28\ pS_{par} + 2.01\ pS_{pred} - 9.17$ explained about 99 percent of the variation in S_P.

S_P decreased from the 1964-65 generation on five of the six plots. On each of these plots, mortality due to parasitism and predation increased, and mortality due to unidentified factors increased or remained about the same.

During this period, a group of hymenopterous parasitoids, mainly Ichneumonidae, attack and kill the pupae. Occasionally chalcids or pteromalids also are reared from collections of pupae and these are tallied as primary parasitoids; they may also be secondary parasitoids.

Phaeogenes hariolus (Cress.) was the most important parasitoid of pupae on all plots where an adequate assessment of parasitism was possible. Itoplectis quadricingulatus (Prov.) and Apechthis ontario (Cress.) were numerous in some collections in 1966. Their appearance might be only a function of slightly different timing of collections that year.

During the late pupal period, the budworm is attacked by predators which include late-developing budworm larvae and spruce coneworm larvae. Mortality by these predators tallied in this age-interval cannot be separated from similar mortality caused by the same agents in the previous age-interval. The carcasses remain on the foliage and are probably tallied in both age-intervals.

Birds and squirrels remove pupae from the foliage; this loss is tallied with "other" factors.

Proportion of Females ($P_♀$)

The proportion of female moths varied from 0.30 to 0.62; it was higher on all plots in the 1965-66 generation than in 1964-65.

Several variables related to population density, survival of instar VI and pupa age-intervals, and defoliation were tested for correlation with $P_♀$. Multiple regression analysis indicated that the model

$P_♀ = 10.32 + 0.09\ N_{VI}^{-1} - 3.47\ N_N^{-1} - 1.63\ pS_{pred}$ explained about 78 percent of the variation in $P_♀$.

Of these components, only pS_{pred} was significantly correlated with $P_♀$ indicating that, when the predation of pupae is great, the $P_♀$ is high. This suggests a higher mortality of male instar VI larvae and pupae than of females. This differential mortality probably was due to the more rapid development of male pupae, which made them susceptible to predation by female instar VI larvae and spruce coneworm larvae. The model also indicates that the fewer needles per shoot (N_N), the greater the reduction of $P_♀$. The advanced development of male instar VI larvae may have been synchronized with the appearance of dipteran parasitoids, also. Among the components, VIS_{par} and pS_{pred}, and pS_{par} and pS_{pred} were significantly correlated.

Proportion of Maximum Fecundity (P_F)

Expressions of population density, N_{IV} and N_{VI}, and current defoliation, D_n, were evaluated as variables affecting P_F. Multiple regression analyses showed that none of the independent variables were significantly correlated with the dependent variable or with each other.

Survival of Moths

Greenbank (1963) did not develop a model for the survival of adults because interpretation of the survival percentage is difficult. Adult mortality is not separable from negative dispersal; positive dispersal is detectable only

when more eggs are found on the plot than were expected from pupal densities and fecundity rates.

On the supposition that adult dispersal would be related to densities of larvae and food supplies, S_{IV} and S_{VI} were tested as independent variables. Multiple regression analyses indicated that the model

$$S_M = 7.65 - 1.15\, S_{VI}$$

accounted for about 48 percent of the variation in S_M. The analyses were repeated, substituting the independent variables related to S_{VI}. The model

$$S_M = 17.73 - 3.72\ {}_{VI}S_{par} + 0.94\ N_{VI}^{-1}$$

accounted for about 86 percent of the variation in S_M. Of the independent variables only N_{VI}^{-1} was correlated with the dependent variable; thus, the more instar VI larvae, the lower the survival of moths.

Greenbank (1963) concluded that ". . . dispersal when acting as a mortality factor removes a constant proportion of the population irrespective of its density, but when supplementing populations it adds a proportion that varies with the density of the resident population." Both positive and negative dispersal could occur on the same plot the same year. The combined effect is estimated from the number of moths added to or subtracted from the plot. This appears in the life table as "Normal females × 2" minus "Actual females × 2," each density divided by 2 because only female moths are of concern.

The number of female moths lost from a plot increases with initial population density (Greenbank 1963). This was demonstrated with the life table data. The correlation between the number of "Normal" females and the difference between "Normal" females and "Actual" females is highly significant (r = 0.932). Survival of "Normal females × 2" (S_M) is not correlated with the initial population density, however.

In the life tables, the decrease in population density attributed to adult mortality and dispersal is minimized by the method by which it is computed. The number of "Normal" females is related to the **maximum** fecundity recorded. The number of "Females" and "Actual" females are related to the **mean** fecundity. The loss of "Females" (the number of "Females" minus the number of "Actual" females) is significantly related to the initial population of "Females" (fig. 4). This also demonstrates that the number of moths lost from a plot by dispersal processes depends upon the density of the moth population.

The data gathered in 1965 from the moth traps (fig. 5) help to define the factors in-

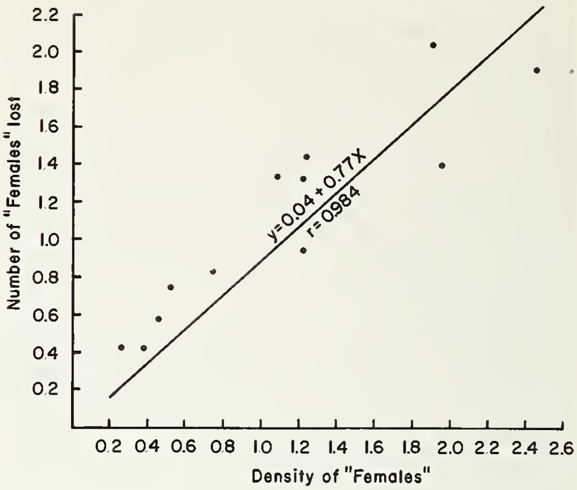


Figure 4. --Relationship between initial density of "Female" moths and number lost from plot.

Figure 5. --More male moths were caught on downhill than on uphill sides of traps baited with virgin female moths.

fluencing flights of male moths. The total number of male moths on the Ophir Creek I study area (14.4 acres) was estimated to be 2,806,042. The percentage of these moths that were available for trapping was estimated from data on emergence and moth longevity. Each total daily catch of moths on the four traps was converted to percentage of available moths, and the percentages were examined in relation to records of temperature and humidity. Graphical analysis showed that neither minimum or maximum temperature nor humidity were related to the percent catch. The moth catch was related, however, to the average temperature between 2000 hours and 2300 hours (fig. 6).

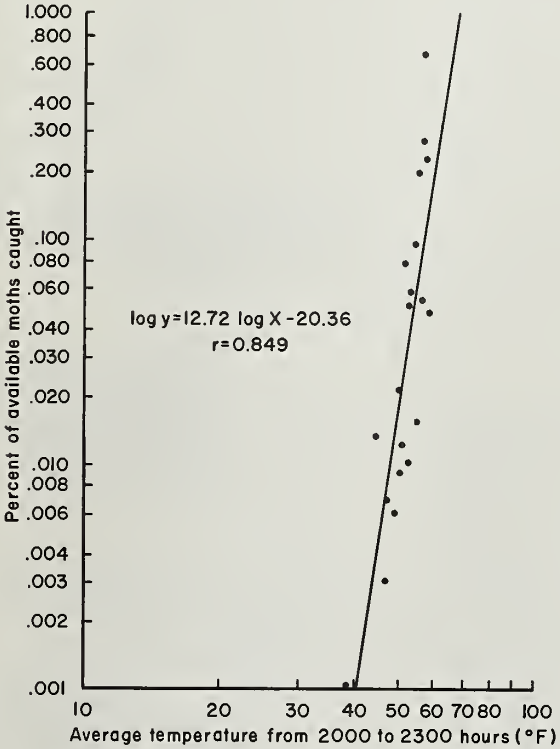


Figure 6.--The relationship between average air temperature and catch of male moths on traps.

Thus a period of low nighttime temperatures could severely limit activity of male moths and, consequently, fertilization of female moths. Greenbank (1963) reported that only minimum relative humidity was correlated with the catch of male moths.

In 1965, about 9 inches of rain fell in a 2-day period during the time of maximum moth availability. Flight activity ceased during this period; many moths, some **in copulo**, were seen drenched but still clinging to the foliage. Many female moths were seen on the ground after the rain ceased. Most appeared to be carrying their full complement of eggs, but were unable to fly; presumably, these females laid no eggs. Despite these adverse conditions, densities of eggs in 1965 were the highest recorded during the study.

SURVIVORSHIP CURVES

Of the 12 life tables, seven were of populations of western spruce budworm with increasing trends (actual trend indices more than 100 percent) and five were decreasing (actual trend indices less than 100 percent). The survivorship curves in figure 7 were based on average life tables for the increasing and decreasing situations, respectively. The differences between them are closely related to the results of the analyses reported earlier.

The average N_E initiating generations of decreasing trends was more than 2.5 times greater than the average N_E initiating generations of increasing trends. Recorded egg parasitism was low; mortality due to unidentified

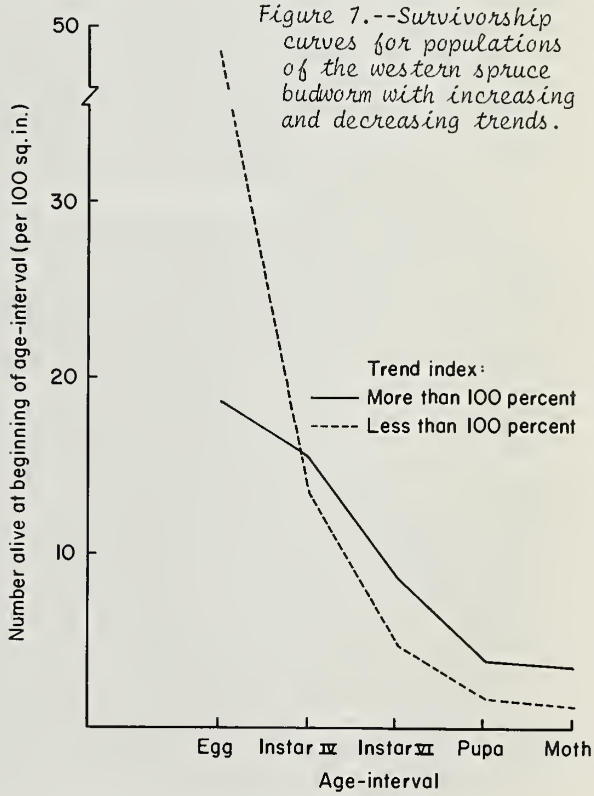


Figure 7.--Survivorship curves for populations of the western spruce budworm with increasing and decreasing trends.

factors was very much greater in decreasing populations, and resulted in very low survival and very high real mortality rates in the egg through instar III age-interval.

The average N_{IV} densities were nearly the same for increasing and decreasing populations. Mortality due to parasitoids was nearly equal but mortality due to unidentified factors was considerably higher in decreasing populations. Although S_{IV} was significantly reduced in decreasing populations, real mortality in the "instar IV through V" age-interval was twice as high in increasing populations as decreasing.

In the "instar VI through early pupa" age-interval, the N_{VI} was nearly twice as high in increasing populations as in decreasing. Parasitism was somewhat higher in increasing populations; mortality due to unidentified factors was again considerably higher in decreasing populations. Real mortality in this age-interval was four times higher in the increasing populations.

In the "pupa" age-interval, mortalities due to parasitoids, predators, and unidentified factors were all higher in populations with decreasing trends. Compared to the preceding age intervals, S_P was relatively high in decreasing populations; real mortality was low.

The percentage of female moths was considerably higher in decreasing populations, but fecundity was nearly 10 percent lower than in increasing populations. Egg deposition was much less in decreasing populations than in increasing. Losses of moths were considerably higher in decreasing populations, largely because of reduced fecundity and about half as many female moths.

Survivorship curves for populations of the western spruce budworm on the three host species are compared in figure 8; four life tables were averaged for populations on Douglas-fir, six for white fir, and two for Engelmann spruce. The curves for Douglas-fir and white fir were similar, as were survival rates, real mortality rates, and fecundities. On Engelmann spruce, N_E was nearly double and S_E was about half as large as on the other host species. In general, mortality due to parasitism and predation was about 25 to 50 percent of similar mortality on Douglas-fir and white fir in all age-intervals. Total mortality on Engelmann spruce in the instar VI age-interval was about 37 percent compared to about 61 and 65 percent on Douglas-fir and white fir, respectively, and, in the pupa age-interval, about 5 percent compared to about 27 and 16 percent, respectively. Adult mortality ± dispersal was slightly higher on spruce. The net

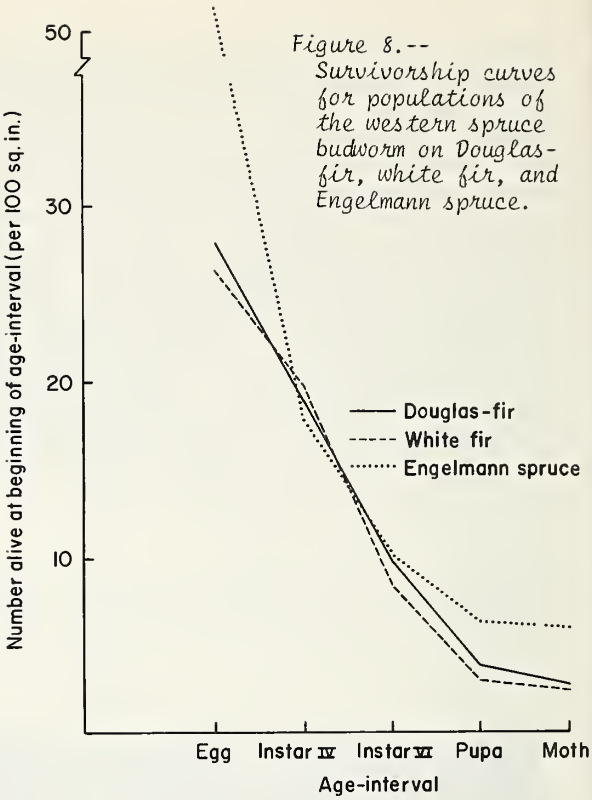


Figure 8.--Survivorship curves for populations of the western spruce budworm on Douglas-fir, white fir, and Engelmann spruce.

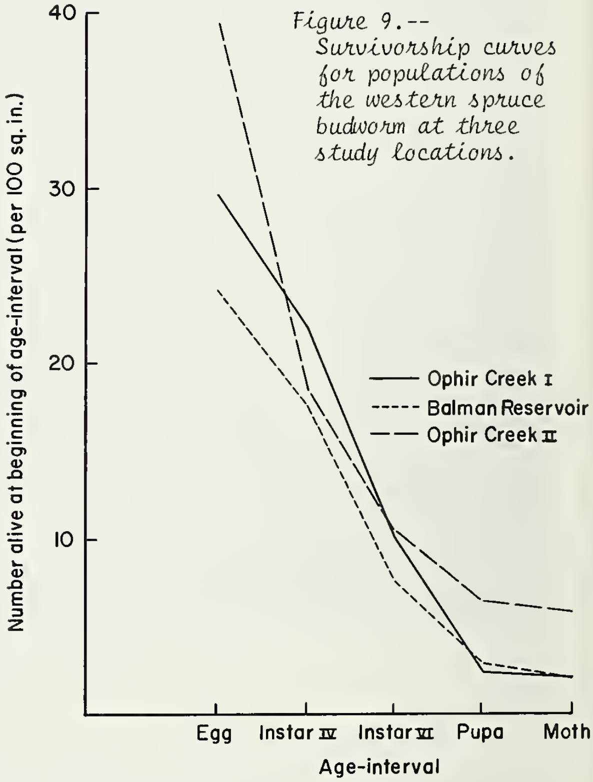
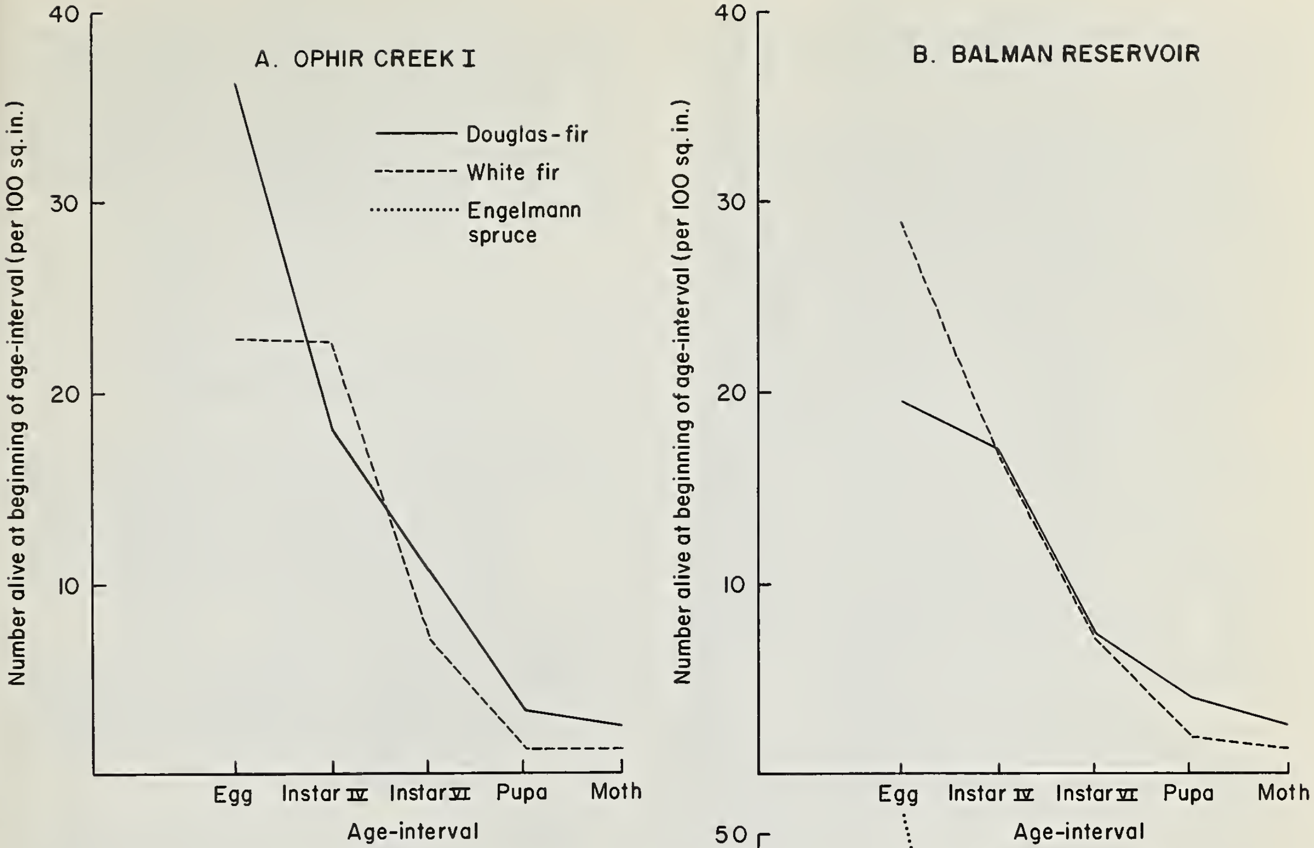


Figure 9.--Survivorship curves for populations of the western spruce budworm at three study locations.



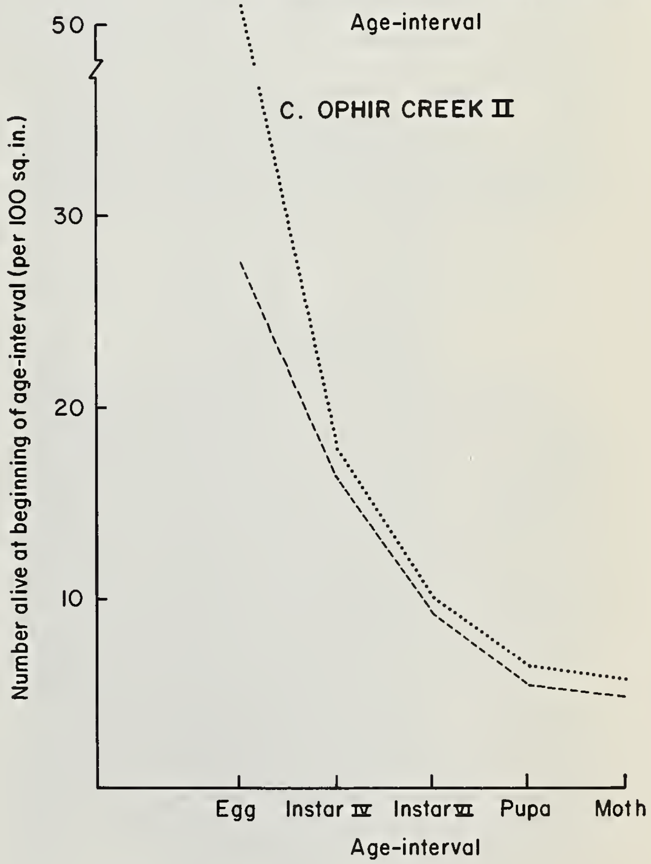


Figure 10.--Survivorship curves for populations of the western spruce budworm on two host species at each of the three study locations.

results were actual trend indices of 98 percent on Engelmann spruce, 111 percent on Douglas-fir, and 105 percent on white fir.

The survivorship curves in figure 9 were taken from the averages of the four life tables at each location. The curves for the Ophir Creek I and Balman Reservoir areas were similar except that parasitism, predation, and total mortality in the pupa age-interval were about double and mean fecundity was somewhat higher at the latter location. As a net result, the actual trend indices were 98 percent at Ophir Creek I and 123 percent at Balman Reservoir.

Populations on Engelmann spruce were studied only at Ophir Creek II, and the differences on that species (noted above) were largely responsible for the differing curve for Ophir Creek II. N_E was much higher and, consequently, S_E was much lower. Parasitism, especially in the instar IV age-interval and the instar VI age-interval, was about half as great; mortality in the pupa age-interval was about

the same as at Ophir Creek I; P♀ was lower. The actual trend index at Ophir Creek II was 266 percent.

The survivorship curves for populations on different hosts at the same locations are compared in figure 10. However, averages of only two life tables per host at each location are of limited value. At Ophir Creek I (fig. 10a) N_E was higher and S_E lower on Douglas-fir compared to white fir. In the instar VI age-interval, parasitism was higher on Douglas-fir but mortality due to unmeasured factors, probably starvation, was high on white fir.

At Balman Reservoir (fig. 10b) populations were initially higher on white fir and survival of the first age-interval was lower. On white fir, mortality due to unidentified causes, probably starvation, was high in the instar VI age-interval and mortality due to predation within the pupa age-interval was especially high. Although final population levels were nearly equal, the actual trend index was 150 percent on Douglas-fir and 104 percent on white fir.

As noted previously, population levels were especially high on Engelmann spruce at Ophir Creek II (fig. 10c); otherwise trends were nearly identical on the two hosts. Mortality due to parasitism in the instar VI age-interval and the pupa age-interval was considerably higher on white fir and P♀ was especially low on this species. Final population levels were nearly twice as high on spruce; actual trend indices were 102 percent on white fir and 98 percent on Engelmann spruce.

IMPLICATIONS

Each year pest control organizations conduct biological evaluations of spruce budworm infestations to determine the probable needs for suppression the following season. These evaluations are usually surveys in late summer or fall to learn if densities of new egg masses are higher or lower than in previous years and the degree of defoliation to be expected. Sometimes data on defoliation in the current year and on growth of the hosts are taken also.

The results of this study indicate that high densities of eggs may foretell decreasing population trends. The critical egg density separating decreasing and increasing populations remains unknown. Actual trends seem to depend largely upon unknown mortality factors during fall and spring periods of dispersal and during the winter months. To add accuracy to biological evaluations, egg mass surveys in late summer or fall should be followed in the spring by surveys when instar IV larvae predominate to determine overwinter survival. Trend and damage predictions can then be updated to confirm suppression needs.

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Most outbreaks of the western spruce budworm (Choristoneura occidentalis Freeman) in the central and southern Rocky Mountains are eventually terminated by natural causes. This study was initiated to identify and determine the relative importance of natural mortality factors. Life tables were prepared for two generations of budworms at three locations on two host species. Relationships between survival rates, fecundities, and sex ratios as dependent variables and budworm densities, survival from parasitism and predation, measures of food supply, and survivals in age-intervals as independent variables were analyzed by multiple regression. Considerable mortality was credited to unknown factors, possibly including infestation-induced changes in food quantity and quality, and weather. Mortality due to these factors was much higher in decreasing populations than in increasing.

Key words: Choristoneura occidentalis, western spruce budworm.

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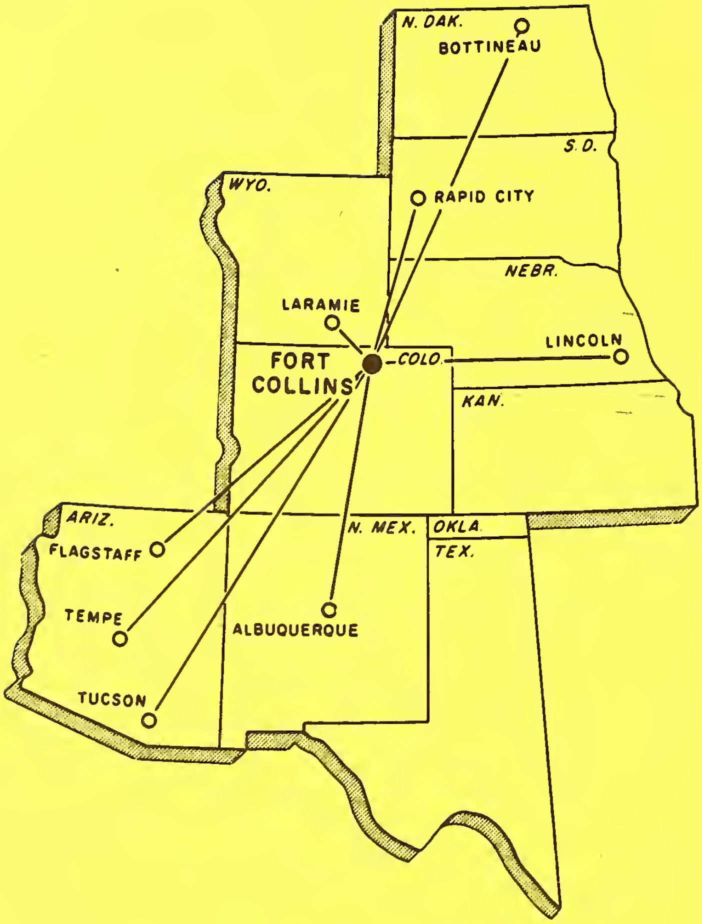
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